Predicting Excretion Rates of Protozoa: Reply to the Comment by Landry

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Predicting excretion rates of protozoa: Reply to the comment by Landry[1]

Landry (1993) has proposed an equation relating protozoan respiration rate and nutrient excretion rate that includes terms for protozoan assimilation efficiencies for C and nutrients (his equation 8). He points out that the use of a simpler equation presented by Caron and Goldman (1988, 1990), Caron et al. (1990), and Caron (1991), which did not consider assimilation efficiencies (equation 1: Landry 1993) may result in significant under- or overestimations of nutrient excretion.

We agree with the intent and conclusion of Landry's emendation to equation 1. He has clearly and convincingly demonstrated the importance of including assimilation efficiencies in these calculations. If one cannot discount the excretion of organic material in the mass

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balance of C and nutrients, then measurements of the assimilation efficiencies for these elements are certainly necessary.

We also agree that the simplification (i.e. that egestion is negligible) which we used in our work with the omnivorous flagellate *Paraphysomonas imperforata* is probably not acceptable with most protozoa and, in the strictest sense, probably not with *P. imperforata*. Studies by several investigators have begun to document the production of particulate and dissolved organic fecal material by phagotrophic protozoa (Stoecker 1984; Andersson et al. 1985; Elbrächter 1991; Nagata and Kirchman 1991). We have ourselves published estimates of the amount of DOM and POM released by protozoan grazing (Caron et al. 1985). Recognition of the potential importance of C and nutrient assimilation efficiencies for predicting nutrient excretion rates as described by Landry is therefore warranted.

The simple fact, however, is that equation 1 is the only *practical* means of relating protozoan respiration and nutrient excretion rates at this time. Assimilation efficiencies are presently unobtainable for most (if not all) protozoa. Several methods have been proposed (and some discarded) for measuring assimilation efficiencies of metazoan zooplankton (references cited by Landry). These difficulties are exacerbated with protozoa. We are aware of only two crude estimates of protozoan assimilation efficiencies (Rassoulzadegan 1978; Stoecker 1984). Both of these estimates were for relatively large ciliates that were fed phytoplankton containing significant quantities of undigestible materials, and which therefore produced fecal "pellets" that could be microscopically or electronically measured. Both methods of estimating assimilation efficiencies were rather indirect, and neither provided accurate estimates of AE_C or AE_N.

We found that egestion of ingested prey was minor in our experiments with *P. imperforata* (Caron et al. 1985). For this reason we felt justified in not considering it in our equation. Our intent was to examine the relationship between the equation resulting from this assumption with empirical measurements of respiration and nutrient regeneration in laboratory cultures. Equation 1 was intended as a simple, conceptual framework for nutrient cycling rather than as a testable hypothesis because in no way would it (or equation 8) be practical for predicting nutrient excretion rates of protozoan assemblages in nature.

Despite our crude assumption that egestion was negligible, we obtained reasonably good agreement between predicted and observed (measured) nutrient excretion rates particularly when the prey were nutrient replete (i.e. $N:C_{prey} \approx N:C_{pred}$). Landry notes that there are several alternative explanations as to why our predicted (from equation 1) and measured excretion rates agreed. We may have slightly overestimated the gross growth efficiency of the flagellate (equation 1 predicts excretion reasonably well at low GGE), or the excretion rates that we observed may have landed fortuitously in the range predicted by equation 1. These are realistic possibilities. In truth, other practical difficulties with performing these experiments also could have confounded the comparison of predicted and measured excretion rates. It is possible that the prey altered its C : nutrient ratios as the experiment proceeded and also affected our determination of the C : nutrient ratios of the protozoan. Changes in these ratios during the experiment would, of course, alter the nutrient excretion rates predicted by either equation 1 or 8 even if assimilation efficiencies remained constant and equal to 1.0. These practical problems in measuring the parameters that *can* be measured (with considerable effort) in nutrient cycling experiments underscore the difficulties associated with obtaining experimental data on this topic.

Landry also suggests that reingestion of egested food particles by *P. imperforata* may have resulted in a situation where its assimilation efficiency in our studies (Goldman et al. 1985; Caron et al. 1985; Andersen et al. 1986; Caron and Goldman 1988, 1990) was ≈ 1.0 (i.e. particulate fecal C was reingested until all prey biomass was assimilated) and that this process was the reason why our predicted and observed excretion rates were so close (equation 8 reduces to equation 1 when $AE_C = AE_N = 1.0$). This possibility (reingestion of fecal material) is speculative but certainly cannot be ruled out in our studies, and it is a valid point to raise. If this situation is true, then approximating the "net" assimilation efficiency of *P. imperforata* as 1.0 and applying equation 1 to approximate the relationship between respiration and nutrient excretion rates was a reasonable, albeit somewhat artificially induced, simplification in our case.

We recognize that equation 8 should eventually replace equation 1 for relating C and nutrient cycling by protozoa when estimates of C and nutrient assimilation efficiency can be made. Overall, we agree with Landry that the problems associated with measuring assimilation efficiencies of protozoa do not justify the tendency of protozoologists to ignore this feature of protozoan growth, nor does it obviate the need to apply the appropriate equation for predicting nutrient excretion. Information on the assimilation efficiencies of protozoa feeding on natural prey is essentially nonexistent, and it will be necessary to address this aspect of their ecology in the future. We concur with Landry that these types of simplifications must be dismissed as methodological developments allow more sophisticated descriptions to be tested.

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